Coupling Behavior and Vertical Distribution of Pteropods in Coastal Waters using Data from the Video Plankton Recorder

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LONG-TERM GOAL

My long-term goal is to understand the biological and physical mechanisms controlling plankton distributions in coastal waters though a combination of in situ observations, experimental manipulations in the laboratory, and numerical simulations of the interaction between plankton behavior and physical gradients.

OBJECTIVES

My objective in this project is to test the hypothesis that the vertical distribution of the pteropod *Limacina retroversa* (Pteropoda, Thecosomata) over its ontogeny is predictable as a function of light, temperature, salinity, food concentration, stratification and mixing intensity. *Limacina retroversa* is an ideal model organism for studies in population dynamics because it has a short two-year life span, swims and sinks in the vertical dimension only, and it has a limited behavioral repertoire.

APPROACH

A combination of empirical, theoretical, and field studies are being used to develop a method for making accurate short-term (hours-days) predictions of the abundance and distribution of *Limacina retroversa* in the ocean. This marine snail occurs in large numbers in coastal waters, forming dense patches many kilometers in length that are acoustically and optically opaque due to the animal's hard shell. A new conceptual approach is being developed to obtain behavioral information on individual plankton over a large range of spatial scales (1 cm-100 km). Still images from the Video Plankton Recorder (VPR) are being used to link behavior at the micro-scale to vertical and horizontal distributions of plankton over much larger scales.
First, a series of mesocosm experiments are being conducted to determine the effects of each of these variables on swimming behavior and vertical position in the water column. Second, still images from the mesocosms using the mini-VPR are being used to infer behavior of individual pteropods. Third, a random walk turbulence model with behavioral feed-back is providing coupling to the population level. And, fourth, the hypothesis is being tested in the field using both moored and towed VPR instrumentation in conjunction with the NSF-GLOBEC Georges Bank Program.

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WORK COMPLETED/RESULTS

Collection and Culture of Pteropods

All the experimental work being conducted in the laboratory requires a consistent supply of pteropods of a variety of developmental stages. This is being addressed through both field collections and laboratory culture programs. Pteropod collections were initiated in March 1996 with the help of numerous investigators in the US GLOBEC Georges Bank Program Broadscale cruises. Four collections of about 5,000 individuals each were made on the Southern Flank of Georges Bank providing sufficient material for lab work throughout the Spring months. Attempts to get *Limacina* into culture were made throughout the season, but survival of the larval stages was poor. During the 1997 GLOBEC field year (March-July) we made 7 independent collections of at least 10,000 adult pteropods each. Together with my Research Associate Phil Alatalo, I have completed numerous lab experiments and now have an F3 generation of *Limacina* in culture. The key to culturing the larvae has been large culture vessels (>12l), low food concentrations (<10^3 cells.ml), mixed algal diet (*Croomonas*, *Isochrysis*, *Hterocapsa*, and *Proocentrum*), and low mixing conditions. Additional field collections were completed during the 1999 GLOBEC field year. We hope to keep *Limacina* in culture for years to come as a consistent supply of material for various experimental studies.

Population-Level Experiments:

Experiments on populations of pteropods in 4 m deep laboratory mesocosms are looking at responses to light, temperature, food concentration, salinity, stratification, and mixing intensity. Continuous observations of population diel vertical migration patterns over periods of weeks are being conducted using video image and image processing techniques. In the absence of food (motile dinoflagellates), predators and strong mixing, *Limacina* appear to be reverse diel migrators moving to the surface 180 degrees out of phase with the light regime (up at the surface during the day and near the thermocline at night). When dinoflagellates are added, the pteropods continue to follow their prey to the surface during the day and lower in the water column at night.

We have conducted several experiments where predators (*Clione* sp.) were added to the mesocosms while DVM was monitored. The hypothesis that *Limacina* will ignore food distributions near the surface in favor of avoiding predation during the daylight hours was unsubstantiated: *Limacina* continued its normal migration pattern in the presence of severe predation pressure by *Clione*. Since Clione is a mechanosensory predator and does not use vision, this result is not surprising, but does demonstrate that predation pressure in not necessarily the key factor controlling DVM.

Individual-Level Experiments:

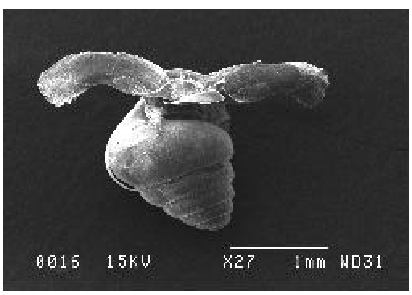
Experiments are being performed on individual pteropods to analyzed their swimming, sinking and feeding behavior, the kinematics of motion, and ecological energetics. Individual pteropods are followed in a 4 m-deep tank for periods of up to eight hours while observing swimming/sinking speeds and parapodia positions and other behaviors. This information is essential as input into the IBM simulation models being developed below.

A complete data set has now been collected describing parapodia position and the instantaneous swimming behavior of an individual as a function of organism size. Based on the angle the parapodia makes with the gravity vector, we can now infer with 99% accuracy the swimming behavior (swimming or sinking) and the relative speed and direction. This information

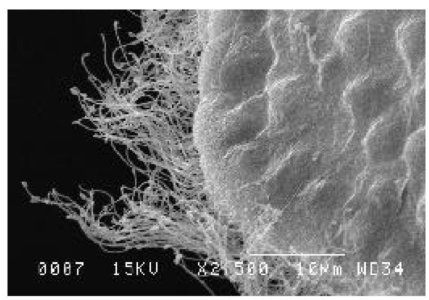
is critical for extracting behavioral information from the still VPR images described below.

High-speed video observations of the feeding process in juvenile and adult pteropods show clearly that phytoplankton prey are captured on the dorsal surface of the parapodia through interaction with cilia during the sinking phase when the parapodia are held dorsal to the shell. Captured cells are transported to the mouth through an extensive network of ciliated channels leading from the tips of the parapodia. Moreover, individual cells may be selected for ingestion following capture. This description of feeding behavior is in contrast with the mucus web observations of feeding reported in the literature. We have never seen a mucus web in the laboratory or in VPR images from the field. Thus, there is more than one mode of feeding which may depend on local particulate conditions or other environmental characteristics.

The energetics of swimming/sinking, feeding, mating, etc. are being measured on individual pteropods as input to the simulation models described below. Tall but narrow polarographic respiration chambers allow individuals to behave reasonably normally as oxygen utilization and behavior is monitored. These data are being taken over a wide range of developmental stages (larvae-adult) and temperatures. One of our most recent and fascinating findings is that pteropods switch between muscular swimming by sculling with their parapodia to ciliated swimming when they hold their parapodia still. From the observer's perspective, when the peropodia are held motionless above the shell, the animal can either sink like a rock at 2-3 $cm.s^{-1}$ or they may float around appearing to have attained neutral buoyancy. Close examination of the ciliation on the edge of the parapodia and the flow field resulting from the beating of these cilia shows that the cilia are responsible for holding the pteropods position in the water column, not a mucus web as stated in the literature.



SEM of adult Limacina retroversa



SEM of lateral cilia along the margin of the parapodia responsible for locomotion and feeding.

Growth and developmental rates are being quantified from hatching through senescence using high-speed video microscopy, thick-section histology, and Scanning Electron Microscopy. SEM images are invaluable for describing the three-dimensional pattern of ciliation on the parapodia used during food collection and swimming.

Field Distributions and Behavior:

In this component of the project, the still images of the VPR are being used to infer an instantaneous behavior associated with parapodia position. We have finished the re-analysis of VPR 22 transect across Great South Channel (Gallager et al., 1996. Deep Sea Res. II. 43:1627-1663) for zooplankton postures. Appendage and orientation of all zooplankton along that transect are being classified manually. In addition we have recently completed a series of cruises with the

VPR to Georges Bank in which many pteropods were sighted. One particularly exciting study was done in June 1997 when a patch of copepods and pteropods were followed for a period of 48 hours while quantifying their horizontal and vertical distribution in real-time with computers on board ship. The more than 10,000,000 images extracted and processed for organism abundance during that study are now being re-processed for posture and orientation information. The data obtained from these field collected images will be combined with the kinematic studies outlined above to produce spatial maps of zooplankton behavior over the transect. The simulation models (below) will then be used to simulate and project those populations days into the future knowing the individuals responses to environmental gradients.

Simulation modeling:

Together with Dr Hidekatsu Yamazaki and his wife Atsuko Yamazaki I have developed an Individual Based Model for simulating the vertical trajectory of pteropods as a function of internal state (hunger, energy levels, etc.), external food, light and temperature to govern swimming and sinking patterns. The results are very exciting- the model shows very clear resemblance to the individual behaviors observed in our tanks in both frequency space and over time. Coupling the behavioral model with an Ekman mixed layer model for production of turbulence is in progress.

IMPACT/APPLICATION

There are a number of direct applications of the data and simulation models being developed in this project. Since plankton aggregations strongly affect acoustic and light scattering in the ocean, knowledge and prediction of plankton distributions is crucial to successful interpretation of acoustic backscatter data obtained in situ, and remote optical measurements. Predicting the likelihood of plankton aggregations causing false targets in mine countermeasures warfare could be a cost-effective and life-saving operation. Baleen whales congregate while feeding on plankton aggregations. The ability to predict when and where plankton are likely to aggregate based on meteorological and oceanographic measurements could be associated with whale distributions thus diminishing the chances of mistaking them for targets. Finally, understanding the mechanisms controlling plankton distributions is fundamental to long-term predictions of ecosystem dynamics in the face of global change. The work supported by this contract is contributing valuable information towards our understanding of these dynamic processes.

RELATED PROJECTS

Projects related to my YIP study include: 1) Real-time quantification of plankton abundance, size and taxonomic composition using the Video Plankton Recorder, Davis, Gallager, Stewart PIs. funded by ONR. 2) Characterization of the zooplankton community and size composition in relation to hydrography in the sea of Japan, Ashjian, Davis, Gallager PIs. funded by ONR. Both of these projects have benefitted from my YIP award through a more thorough understanding of behavioral information extracted from the still images of the VPR.

PUBLICATIONS

Gallager, S.M. Behavior of individual zooplankton and their meso-scale distribution Submitted